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How Deep Should You Squat to Maximise a Holistic Training Response? Electromyographic, Energetic, Cardiovascular, Hypertrophic and Mechanical Evidence

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Additional information is available at the end of the chapter

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1. Introduction

Skeletal muscle possesses the ability to change its structural and mechanical characteristics in response to its external environment (i.e. it is adaptable). The exact nature of such adaptations is manipulated by, amongst other things, the mechanical stimulus provided to the said muscle. Resistance exercise is an example of one such stimulus, and is used in a variety of settings, such as athletic performance, general health and fitness, injury prevention and rehabilitation. It is also now commonplace for resistance exercise to be used to offset the debilitating effects of illness, disease and sarcopenia (the latter being a term used to describe the age-related loss in muscle mass, which is also accompanied by increased fatty tissue infiltration and the ensuing decrement in muscle 'quality'). The objectives of the resistance exercise protocol therefore, will vary due to the unique nature of each setting, and therefore should be optimised in order to bring about a specific and desirable set of adaptations. Frequent adaptations that are sought from resistance exercise regimes include an increase in muscle cross-sectional area (CSA) and strength [1], alterations to muscle architecture (spatial arrangement of muscle fibres within a muscle [2]), and greater maximal activation of the musculature [3].

Muscle activation has been widely assessed using surface electromyography (SEMG), and in many cases is expressed as a relative level (%) of maximal voluntary contraction (or MVC). It comprises the sum of the electrical contributions made by the active motor units in proximity to the measurement site. The global characteristics of the surface EMG, such as its amplitude and power spectrum, depend on the membrane properties of the muscle fibres as well as on

the timing of the single fibre action potentials. Thus the surface EMG reflects both peripheral and central properties of the neuromuscular system [4]. For many muscles, optimal firing rate, which is that elicited by a maximal voluntary effort, is sufficient to generate a fused tetanus in individual motor units. In predominantly fast-twitch muscles (e.g. biceps brachii), this firing rate is ~30Hz whereas in predominantly slow-twitch muscles (e.g. soleus), this firing rate is ~10Hz [5]. This electromyographic signature is warranted in order for the muscle to express its maximal force generating capabilities, and there have been many studies carried out that have reported a significant increase in agonist SEMG recordings following a resistance training program in both males and females, and in the young as well as the elderly [3, 6-12]. As mentioned previously, muscle adapts in a specific manner to the stimulus provided, and in the case of the aforementioned studies, increases in agonist muscle activation has been shown to be specific to the mode of muscular contraction employed during the resistance training period, and has been fairly well characterised. It is however unclear whether chronic changes in the magnitude of the EMG signal occur with training.

One aspect of resistance training that is scarcely reported in the literature is the acute (and/ or chronic) responses to resistance training programs whereby the length of the muscle when it is loaded is being manipulated. Acutely, it has been demonstrated that there are significantly different responses to exercising at different joint-angles (and thus different muscle lengths). De Ruiter et al. [13] showed that during isometric MVC exercise at 30°, 60°, and 90° of knee flexion, maximal activation of the knee extensors was significantly greater at 90° than the other two angles, despite having identical torque production as 30° (90°; 199±22Nm, 30°; 199±29Nm) and significantly lower torque production than 60° (298±41Nm). A subsequent study [14] found that maximal muscle oxygen consumption was reached significantly later, and was on average ~60% less at 30° compared to 60° and 90° knee flexion. Furthermore, Hisaeda et al.[15] found that when performing isometric contractions at 50% MVC to failure at either 50° or 90° of knee flexion, endurance time was significantly shorter at 90° than 50°. This effect was present both when the exercise was performed with the local circulation occluded and not occluded, thereby highlighting local events as being key to the performance of the musculature at discrete knee angles (or muscle lengths). In addition to this, the slope of the iEMG-time to fatigue regression was significantly greater in the 90° condition compared to 50°. It is proposed that one of the reasons for an increase in oxygen consumption at longer muscle lengths (or more flexed joint angles) is that to produce the same external torque, the internal mechanical stress must be higher at more flexed angles (90°) compared to extended angles (30° or 50°) because the moment arm of the in-series elastic component (i.e. the distance between the tendon and the joint centre of rotation, a factor which impacts on the forces required at the muscle) is shorter [16] at more flexed angles. The above studies provide compelling evidence of the link between the muscle length during a bout of resistance exercise and the acute impact on muscle activation levels, energetic provision, fatigability, as well as torque production. It has therefore been important to determine the nature of the acute effects of length-specific training because it is the accumulation of the acute responses that ultimately are reflected in the chronic muscle adaptations (known as the repeated bout effect).

Previous investigations have also identified the link between muscle length (or joint-angle) and gains in strength and/ or levels of muscle activation following more extended periods of resistance training [17-21]. Briefly, these studies have shown that significantly greater increases in isometric strength are attained when tested at the training length or position, and that these changes in strength are accompanied by significantly greater activation of the muscle at the training position. Furthermore, several studies have outlined that at shorter muscle lengths, the phenomenon of length-specific adaptations are more marked compared to those at longer muscle lengths [19, 21]. For example, performing resistance training at a shorter muscle length results in increases in strength at, and close to the training muscle length, whereas training at longer muscle lengths results in strength increases at, and around a larger range of muscle lengths. However, all of the above data is provided via controlled isometric (static) contractions, when resistance training programs for most individuals are predominantly of a dynamic nature, and therefore warrants further research to extend the knowledge in this area. Therefore the aims of the body of work presented for the first time here were:

1. To describe the acute differences in activation of the Vastus Lateralis (VL) muscle whilst performing dynamic resistance exercise over relatively short muscle lengths compared to long muscle lengths; here comparisons were carried out a) where the external 'perceived' workload is matched, and b) when the internal workload is systematically matched between the two training modalities.
2. To describe the changes in oxygen consumption and cardiovascular responses during these exercise protocols.
3. To identify any link between the acute responses to loading at shorter vs longer muscle lengths; and the more chronic adaptations on VL muscle activation following 8 weeks of length-specific resistance training and 4 weeks detraining.

2. Methods

2.1. Acute study

Ten males (23 ± 3 years, 1.79 ± 0.06 m, 73.4 ± 8.4 Kg) gave written informed consent to take part in the study. All procedures and experimental protocols were approved by the Ethics Committee at the Manchester Metropolitan University. Exclusion criteria for participation in the study were the presence of any known musculoskeletal, neurological, inflammatory or metabolic disorders or injury. Participants were physically active, involved in recreational activities such as team sports, and had either never taken part in intensive (more than two hours a week) lower limb resistance training or not within the previous 12 months. Participants attended the laboratory for a total of five occasions. The first visit included demonstration of the appropriate squat technique for a standard barbell back squat, and familiarisation of the exercise protocol and testing equipment. The following week participants returned on four occasions, firstly to record their one repetition maximum over each range-of-motion, which was defined as the maximum amount of external weight (Kg) that could be lifted in a controlled manner through the entire range-of-motion, and their MVC on an isokinetic dynamometer (Cybex, Phoenix Healthcare Products, UK) at 50° and 90° of knee flexion. The time-line of the sessions was as follows: Day 1; 1RM & MVC, Day 2; Rest, Day 3; Protocol 1, Day 4; Rest, Day 5; Protocol 2, Day

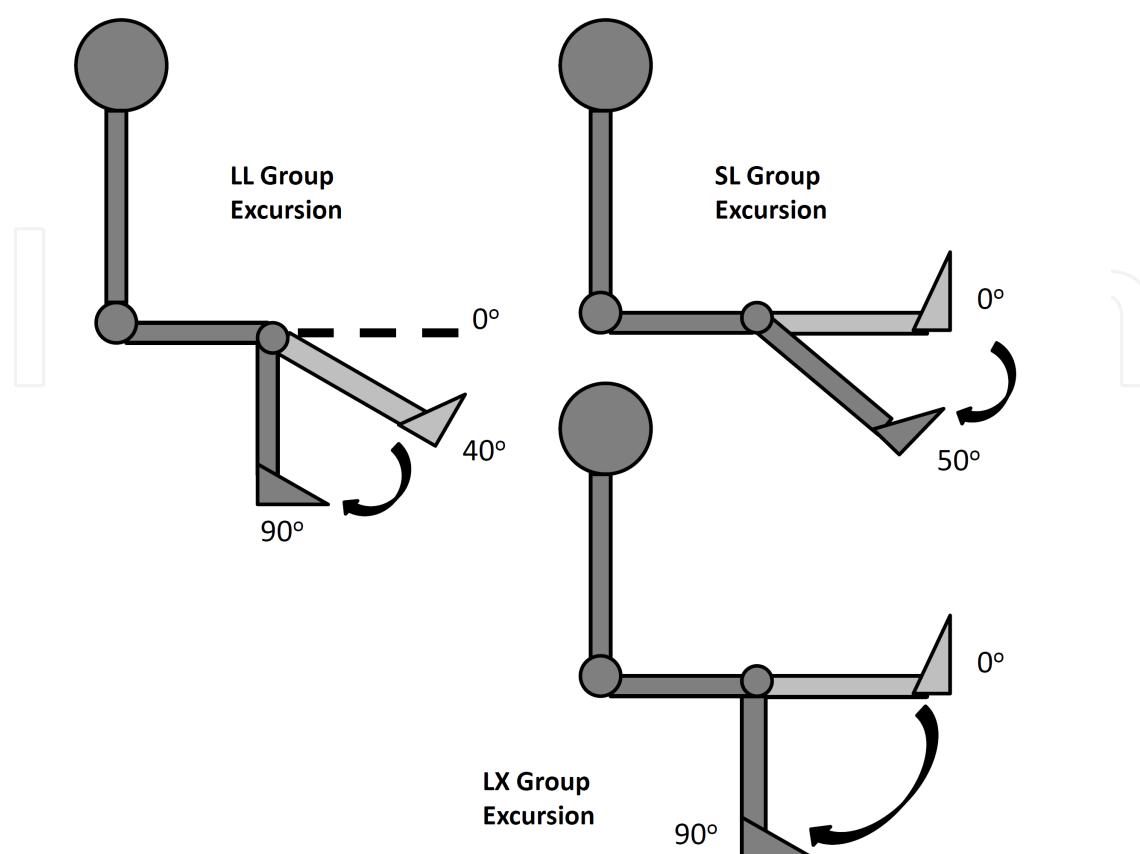


Figure 1. Diagram showing the various knee-joint ranges-of-motion used in the training protocols with a view to describe both acute and chronic training responses

6; Rest, Day 7; Protocol 3. During each of the resistance exercise protocol days, the participants were randomly allocated to perform the resistance exercise session of one of the three designated ranges-of-motion. During each of the resistance exercise sessions, all acute variables (EMG, VO_2 , heart rate, blood pressure) were measured.

Exercise Protocols; Each exercise protocol involved performing exercise over one of three ranges-of-motion (Figure 1). The three ranges-of-motion were; 0-50° knee flexion (shorter muscle lengths, SL), 40-90° knee flexion (longer muscle lengths, LL) and 0-90° knee flexion (complete range-of-motion incorporating shorter and longer muscle lengths, LX). A goniometer was attached to the knee joint centre of rotation, from which the investigator confirmed each angle was met during exercise performance. Each exercise session required participants to perform one set of five repetitions back squats at an absolute load of 20Kg, 40Kg and finally 60Kg. Sets were interspersed by two minutes of recovery. Following a further ten minutes rest, each participant performed a further set of five back squats at 40%, 60% and 80% 1RM, interspersed by two minutes of rest.

Electromyography; A pair of self-adhesive Ag-AgCl electrodes 15 mm in diameter (Neuroline 720, Ambu, Denmark), were placed on clean, shaved, and previously abraded skin, in a bipolar

configuration with an inter-electrode distance of 20 mm. The electrodes were placed at 50% of femur length and 50% of muscle width of the *Vastus Lateralis* muscle (VL). The reference electrode (Blue sensor L, Ambu, Denmark) was placed on the lateral tibial condyle. The raw EMG signal was amplified and bandpass filtered between 10-500 Hz (MP100, Biopac Systems Inc., USA) with a 50Hz notch filter, and sampled at 2000 Hz. All EMG and torque signals were displayed in real time in AcqKnowledge software (Biopac Systems Inc., USA) via a PC (iMac, Apple Inc., USA). The root mean square (RMS) EMG activity was averaged for a 500ms period which coincided with the plateau of peak torque of all analysed muscle contractions.

Oxygen Consumption (VO₂); Gases for VO₂ consumption were collected using standard Douglas Bag techniques. Prior to the beginning of each set of exercise, a clip was placed on the nose of the participant, the Douglas bag mouthpiece was inserted into the mouth and the valve on an empty bag subsequently opened. After the set of exercise was completed, 30 seconds were allowed to elapse before the valves were closed. This was to allow for any excess post-exercise oxygen consumption during the immediate recovery period. A separate Douglas bag was used for every set of exercise completed. Each bag was analysed using a gas analysis program (Servomex 5200 Multiuse, Crowborough, UK) and was used to calculate the FECO₂ and FEO₂ percentages. For these calculation, the data from Gas which had been evacuated for 60 s with a flow rate of 2.1 L/min, the total gas volume which was obtained using a Harvard Dry Gas vacuum (NB. the flow rate (2.1 L) was added to the final figure to give the VE stpd (L/min⁻¹)), the time period in which the Douglas bag was open (secs), load (kg) and subjects' heart rate were all inserted into the gas analysis programme. The VO₂ (ml/kg⁻¹/min⁻¹) was also recorded.

Heart rate & Blood Pressure; Heart rate and blood pressure were recorded at rest in the supine position before the onset of exercise using a standard heart rate monitor (Polar, UK) and electronic blood pressure monitoring device (Panasonic Diagnostec, UK). These parameters were also measured immediately post-exercise, after every set of exercise. Rate of perceived exertion (RPE) was also recorded following the conclusion of each individual set of exercise.

2.2. Chronic resistance exercise program study

Thirty two activity-matched participants were allocated to a training group – SL (shorter muscle length 0-50°; 6 males, 4 females; aged 19±2.2 years, 1.76±0.15m, 75.7±13.2Kg), LL (longer muscle length; 5 males, 6 females 40-90°; 21±3.4 years, 1.75±0.14m, 74.9±14.7Kg) or LX (Whole range of motion, 6 males, 5 females 0-90°; 19.2±2.6 years, 1.71±0.11m, 73.8±14.9Kg). Ten participants (6 males and 4 females; 23±2.4 years, 1.76±0.09m, 77.9±13.1Kg) were assigned to the non-training control group (Con), and continued their normal habitual activity throughout the study period. A One-way ANOVA revealed that the population was homogeneous at baseline for all parameters of interest (P>0.05). All groups were assessed at baseline (week 0), post-training (week 8), after two weeks of detraining (week 10) and following a further two weeks of detraining (week 12).

Electromyography; Preparation of EMG site, measurement and assessment of EMG were as described in the previous section. In addition to these measurements, EMG of the biceps

femoris was also recorded during graded maximal contractions in order to assess antagonist muscle co-activation.

Resistance Training Program (RT); RT was carried out 3 days per week for 8 weeks and ceased during the 4 week detraining period. RT included performing 3-4 sets of 8-12 reps (depending on the stage of the training program) of exercises designed to overload the knee extensors muscle group. Exercises included the barbell back squat, leg extension, leg press, Bulgarian split squat, and forward lunge. 1RMs were assessed and recorded every two weeks to progress the exercise loads.

Muscle size measurements; VL muscle widths were measured using B-mode ultrasonography (AU5, Esaote Biomedica, Italy) at 25%, 50% and 75% of femur length. The ultrasound probe was held in the transverse plane and used to locate the borders of either side of the VL muscle. Each of these junctures was marked on the skin and the distance between them measured. In addition, at each of the aforementioned sites, thigh girths were also measured using standard anthropometric techniques. All data is presented as mean \pm standard deviation (S.D.).

Muscle strength measurements; Throughout the training program, 1RM of the knee extensors systematically monitored on a knee extension machine (Technogym, Bracknell, UK).

3. Results

3.1. Acute responses

Muscle Activation; As expected *Vastus lateralis* activation increased linearly with absolute external load, with activation being significantly greater ($P < 0.05$) when lifting 40Kg compared to 20Kg, and also when lifting 60Kg compared to 40Kg ($P < 0.05$) and 20Kg ($P < 0.001$). When comparing activation between ranges-of-motion as a percentage of MVC, activation of the muscle was significantly ($P < 0.05$) less at SL ($59 \pm 6\%$, $63 \pm 7\%$) compared to LL ($73 \pm 7\%$, 77 ± 5) and LX ($70 \pm 7\%$, $75 \pm 6\%$) at 40Kg and 60Kg loads respectively (Figure 2A). During relative loading, performing exercise at 60% 1RM did not increase activation compared to 40% 1RM ($P > 0.05$), though activation was increased at 80% 1RM compared to 60% ($P < 0.05$), and 40% ($P < 0.001$). There were no significant differences in activation at 40% and 60% 1RM between the three ranges-of-motion ($P > 0.05$), whilst at 80% 1RM, VL activation was significantly greater during exercise in LL and LX compared to SL (Figure 2B; $P < 0.05$). It is notable that these effects were similar for all two 'long muscle' training protocols so that there were no significant differences between the longer muscle length ROM and the complete ROM under any loading conditions ($P > 0.05$).

Oxygen Consumption (VO_2); There was no significant changes in VO_2 between any of the absolute loading conditions or between any ROM ($P > 0.05$). Furthermore, in the relative loading conditions, mean VO_2 was significantly greater at 80% 1RM compared to 40% 1RM (6.4 ± 0.9 ml/kg⁻¹/min⁻¹ vs. 9.93 ± 1.3 ml/kg⁻¹/min⁻¹, $P < 0.05$). VO_2 was greater at 40% and 60% 1RM in LL and LX than SL, however there were no significant differences between these ROMs. At 80% 1RM there was a significantly greater VO_2 (Figure 3) in the LL ROM compared to SL ($P < 0.05$),

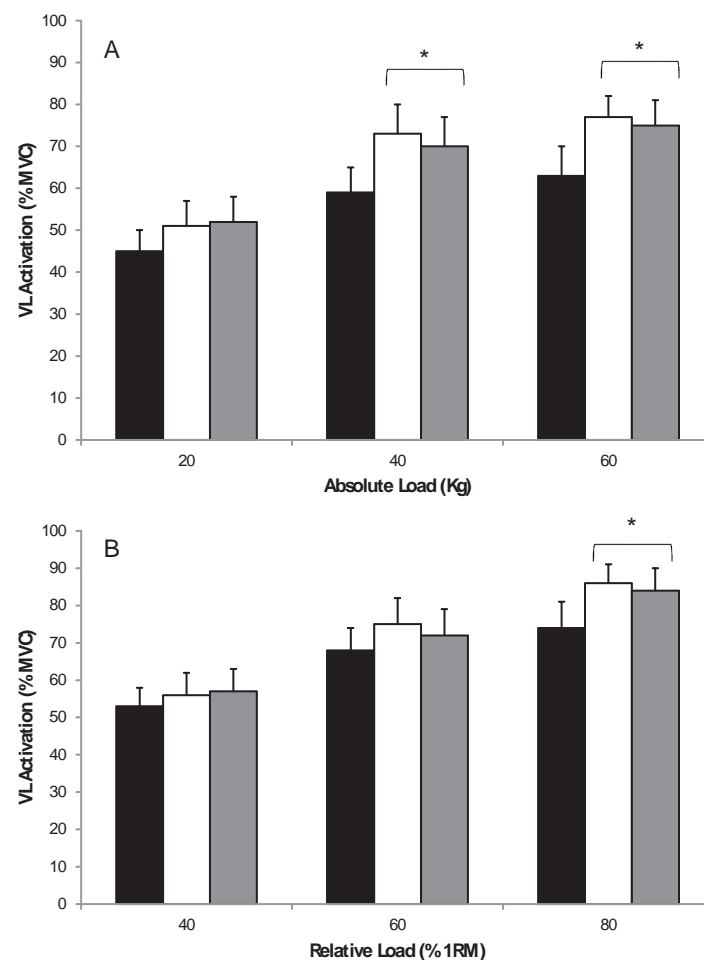


Figure 2. Vastus Lateralis activation in SL (black bars), LL (white bars) and LX (grey bars) following varying magnitudes of absolute and relative loading. * Significantly different to SL

however there were no significant differences between LL and LX, or SL and LX at this loading intensity ($P>0.05$).

Heart rate & Blood Pressure; There was a significantly greater ($P<0.05$) mean heart rate difference between LL (139 ± 10 beats per minute) and LX (136 ± 11 bpm) compared to SL (118 ± 12 bpm) in both absolute and relative loading conditions, with no difference between LL and LX ($P>0.05$). Mean systolic blood pressure yielded no significant differences ($P>0.05$) between the three ROMs under relative loading conditions, however LX (148 ± 8 mmHg) mean systolic blood pressure was significantly greater than both SL (138 ± 6 mmHg) and LL (135 ± 8 mmHg) following loading under absolute loads ($P<0.05$).

3.2. Prolonged resistance training responses

Agonist (VL) Muscle Activation; Figures 4 and 5 shows absolute (i.e. raw RMS_EMG signal) and relative (i.e. RMS_EMG normalised for values at baseline) changes in muscle activation at baseline and post-training. At week 8, absolute maximal agonist activation did not appear

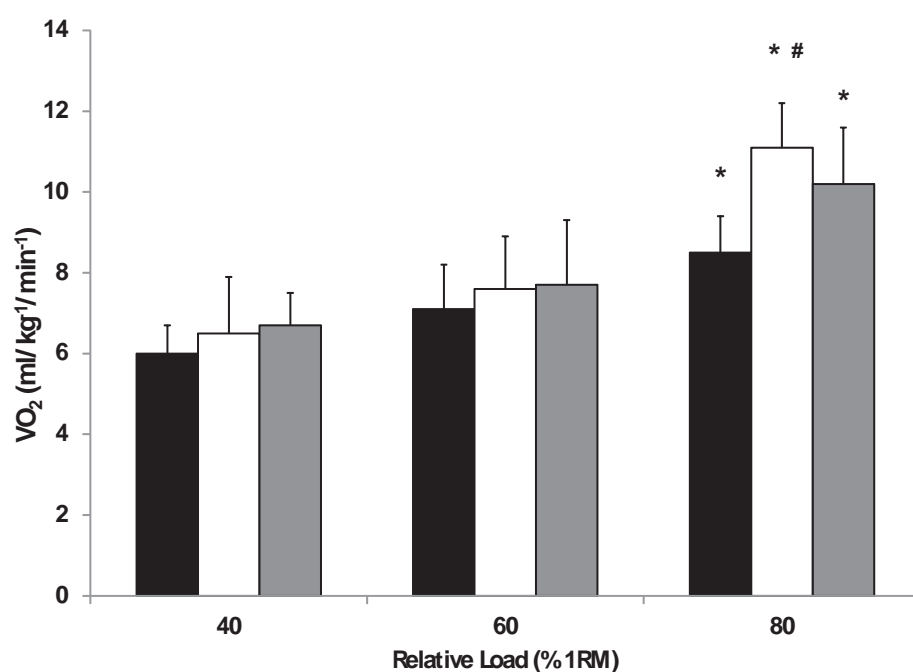


Figure 3. Oxygen consumption (VO_2) during relative loading in SL (black bars), LL (white bars) and LX (grey bars). * Significantly different to 40% 1RM. # Significantly different to SL.

to increase significantly in chronic response to the training protocols, with no significant difference between training groups at any knee angle ($P > 0.05$, Figure 4). However, on further investigation, it was found that in fact, post-training there was a significant relative increase in activation at 50° ($23 \pm 15\%$, $P < 0.05$), 70° ($26 \pm 15\%$, $P < 0.01$) and 90° ($16 \pm 13\%$, $P < 0.05$) in the LX group and at 70° ($24 \pm 9\%$, $P < 0.01$) and 90° ($25 \pm 9\%$, $P < 0.01$) in LL group. In the SL group there was no significant change at 50° , although there were significant ($P < 0.05$) reductions in VL activation at both 70° ($-15 \pm 6\%$) and 90° ($-13 \pm 5\%$). Following detraining, muscle activation at 70° decreased at week 10, and levelled off for the remainder of the detraining period (week 12) in both LL and LX groups with no significant changes compared to week 8. In the SL group, activation reduced at both weeks 8, 10 and 12 compared to baseline, however despite larger decrements in this group, there was no significant differences between all three training groups (Figure 6, $P > 0.05$).

Muscle widths and thigh girths; Changes in muscle widths are shown in Table 1. At week 8, VL muscle widths had increased significantly at all three measurement locations in all training groups compared to baseline ($P < 0.001$). Following the first period of detraining at week 10, the SL group had returned to baseline values at all three measurement sites ($P > 0.05$), however both LL and LX groups retained adaptations at this juncture relative to baseline ($P < 0.01$). At week 12 LX group had returned to baseline levels at 25% and 50% width but still remained significantly hypertrophied at 75% femur length compared to baseline ($P < 0.05$). The LL group retained their significant gains in muscle width at all three sites for the duration of detraining ($P < 0.01$). There were no significant ($P > 0.05$) mean relative changes between training groups

post-training or following detraining at 25% and 50% femur length (SL; $12 \pm 13\%$, LL; $11 \pm 7\%$, LX; $13 \pm 11\%$). However, LL and LX groups had a greater significant ($P < 0.05$) relative increase in muscle width at week 10 (LL; $26 \pm 13\%$, LX; $21 \pm 9\%$) compared to SL ($13 \pm 8\%$) at 75% femur length. This was also the case at week 12, however only LL group was significantly greater ($P < 0.05$) than SL group at this measurement site. Thigh girths increased following training at week 8 in all training groups and at all sites (mean over three sites SL; $3 \pm 2\%$, LL; $4 \pm 3\%$; LX; $4 \pm 2\%$), however this was not significantly different to baseline values ($P > 0.05$) with no differences between groups. Thigh girths also did not differ significantly at weeks 10 or 12 compared to baseline or between groups.

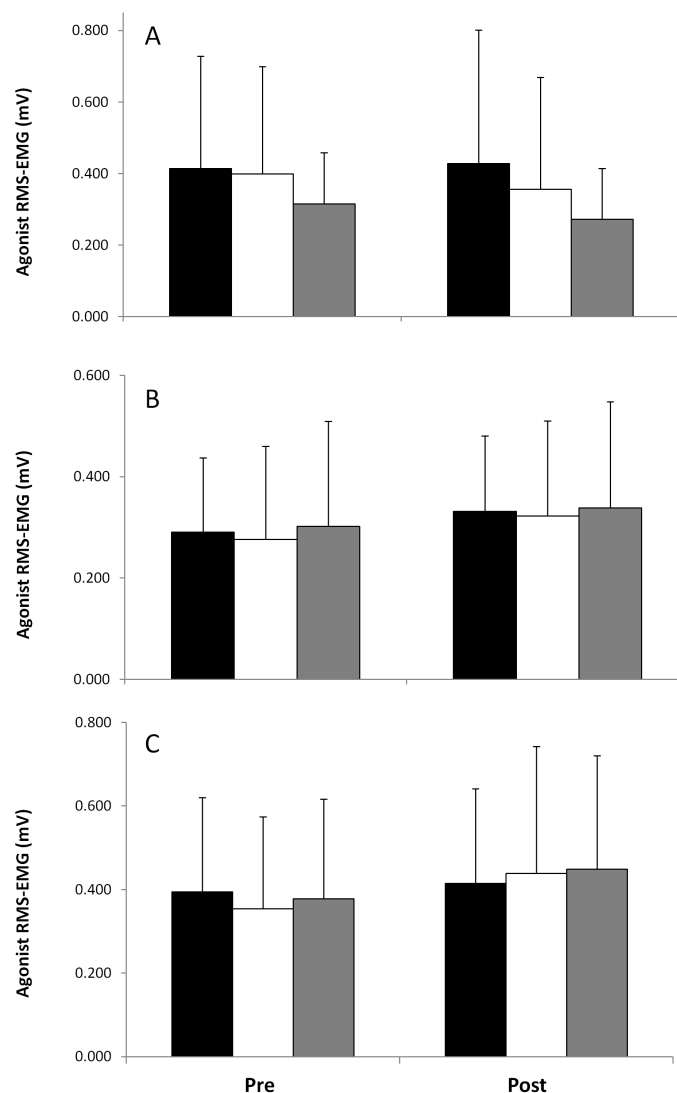


Figure 4. Absolute Changes in VL activation at baseline (pre) and week 8 (post) training at 50° (black bars), 70° (white bars) and 90° (grey bars) knee flexion in A) SL, B) LX and C) LL groups.

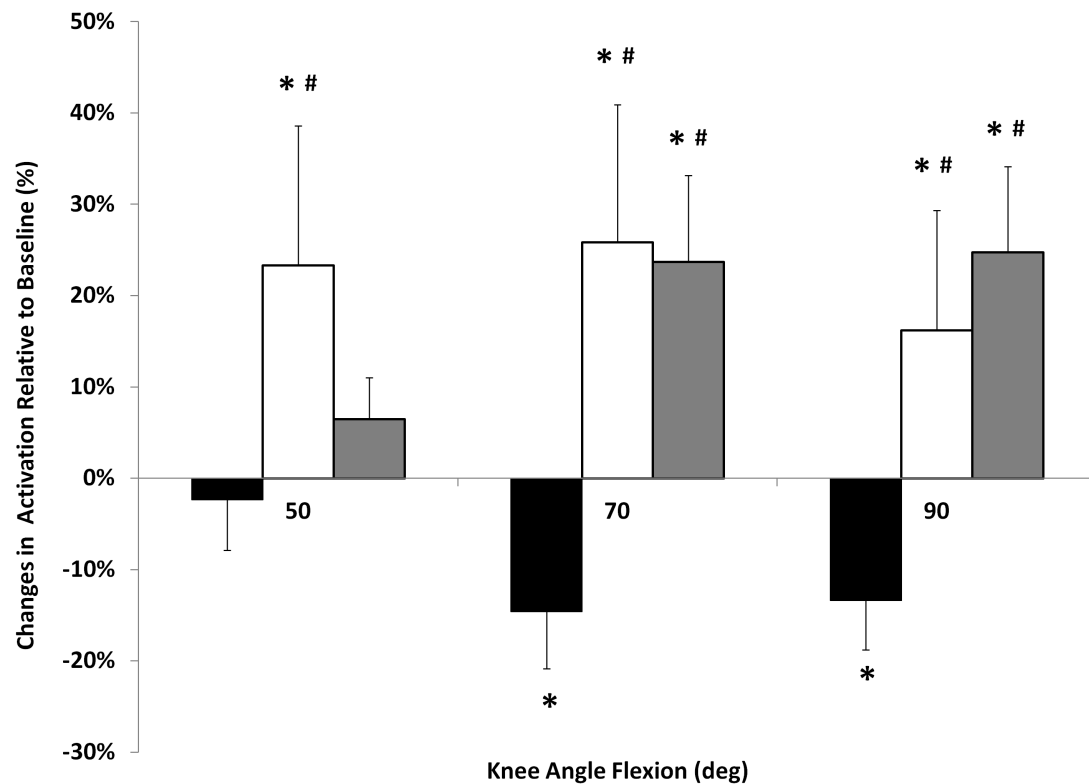


Figure 5. Relative changes in VL activation at week 8 at three knee joint-angles in SL (black bars), LX (white bars) and LL (grey bars). * Significantly different to baseline. # Significantly different to SL group.

Group	% Femur Length	Baseline (cm)	Week 8 (cm)	Week 10 (cm)	Week 12 (cm)
SL	25	12.7±2.3	13.9±2.0*	13.2±1.8	12.9±1.6
	50	12.8±2.7	14.2±2.5**	13.6±1.9	13.3±1.9
	75	9.6±2.2	11.0±1.9*	10.1±1.2	9.6±1.1
LL	25	14.0±1.3	15.3±1.6**	15.6±1.1**	15.3±0.9**
	50	13.8±1.6	15.6±2.0**	15.8±1.5**	15.4±1.3**
	75	9.4±1.8	11.4±1.4**	11.5±1.2**	11.1±1.3**
LX	25	12.2±2.7	14.2±1.9**	13.0±2.0**	12.4±1.8
	50	12.1±2.6	14.3±2.3**	13.1±2.0**	12.3±2.0
	75	8.2±2.2	10.6±1.5**	9.6±1.6**	8.8±1.2*

Table 1. Changes in Vastus Lateralis muscle width at each measurement site throughout training and detraining. * Significantly different to baseline (P<0.05) ** Significantly different to baseline (P<0.01)

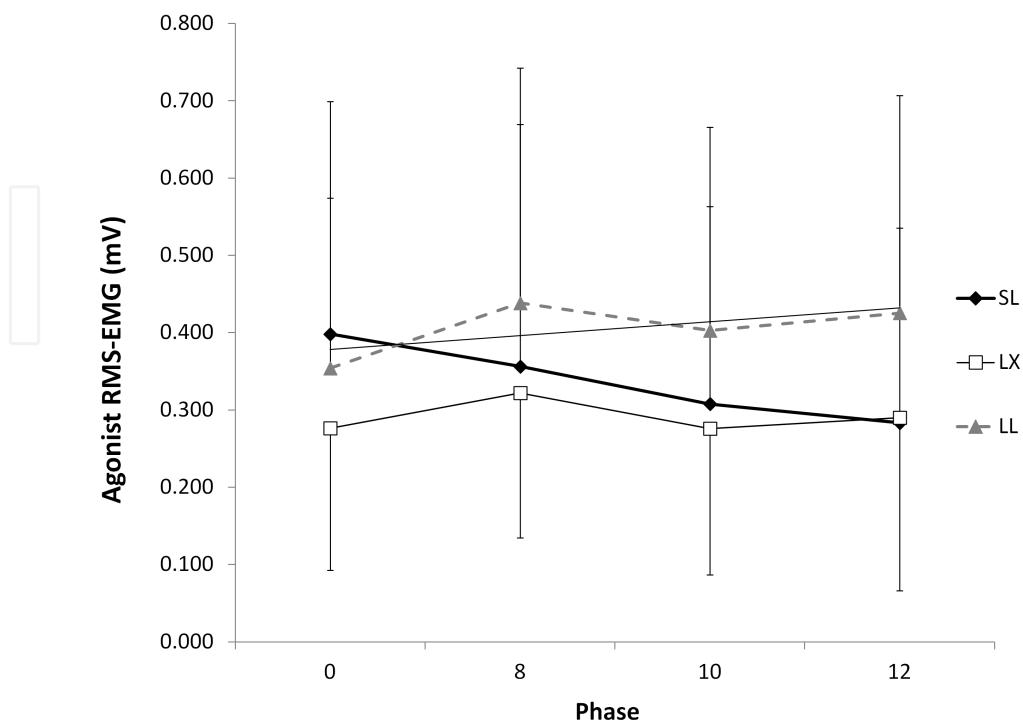


Figure 6. Absolute changes in VL activation throughout training and detraining periods at 70° knee flexion. No significant were detected between phases or training groups ($P>0.05$).

Strength measures; 1RM in knee extension did not increase significantly compared to baseline until week 4 of the training program (data pooled, $P<0.05$) with each training group making similar increments in weight (SL; $11\pm4\%$, LL; $9\pm5\%$, LX $12\pm5\%$). There were further significant increases at week 6 (mean of groups $16\pm6\%$, $P<0.01$) and week 8 (mean of groups $22\pm8\%$, $P<0.001$), with no significant difference in the rate of relative increase in 1RM between groups ($P>0.05$). When muscle activation was normalised against torque at week 8 (Figure 7) as a marker for muscle efficiency, both LL and LX groups showed significantly better improved muscle efficiency compared with SL ($P<0.01$) at 90° of knee flexion, however there were no differences in muscle activation per unit torque at 50° or 70° following training ($P>0.05$). LL and LX were not significantly different to each other in terms of the degree of muscle efficiency increase.

4. Discussion

Resistance training presents a medium through which muscular function can be enhanced. In order to devise an appropriate and effective resistance training program tailored with functional and structural enhancement objectives, it is necessary to understand the responses to both an acute bout of exercise, and the adaptations to exercise over a prolonged period of training. An important aspect for muscular performance is the degree to which the muscle can

be activated. Previous work using isometric contractions of the knee extensors, has demonstrated that the magnitude of maximal muscle activation is dependent on the joint-angle (and thus muscle-length) used during exercise, even when external torque produced is maintained at a similar level at the different joint angles [13]. This earlier study showed that activation of the quadriceps is significantly greater at 90° knee flexion compared to both 30° and 60°, despite isometric MVC torque being significantly less than 60° and identical to 30°. In the current study, unlike previous research, our participants exercised dynamically over a range-of-motion that was predominantly over shorter muscle lengths (0-50°), longer muscle lengths (40-90°) or over both short and long muscle lengths (0-90°) during exercise using absolute and relative loading patterns. During absolute loading, weight lifted increased in a graded manner, and was reflected by significantly increased muscle activation between each absolute load in the training groups. This result was a more easily predicted outcome and reflects one of the fundamental properties of the neuromuscular system, i.e. the size principle [22], where a greater number of motor units are recruited in order to meet the increasing demands of force production. When exercising over longer muscle lengths (LL) and the complete ROM (LX), muscle activation was significantly greater during absolute and relative loading compared to shorter muscle lengths (SL). So why would a muscle exhibit greater activation whilst moving the same external weight but at different muscle lengths? By moving through a range of muscle lengths or joint-angles, the moment arm of the in-series elastic component (i.e. the tendon) also changes. As the amount of force needed to lift an external load (F) is $F = f \times d$, where f is the internal force produced by the muscle and d is the length of the moment arm, when d is greater f will be smaller and vice versa, and therefore when the external force produced is the same but the moment arm (d) is smaller, the contribution from internal muscle force production increases. An example of this experienced in daily living is the increased difficulty in rising from a low seat position compared to a higher seated position. It has been demonstrated previously that when the joint-angle in the knee extensors is at 90° flexion (such as the end of LL and LX group ROM), the moment arm is considerably shorter [16] than when at 50° (the end of SL ROM). Therefore when exercising at 90°, internally the muscle must produce a greater amount of contractile force to overcome the external weight than that required at 50° knee angle. Again due to the overloading principle of training response, a larger number of motor units will have needed to be recruited to match the force demands at the longer muscle lengths, reflected by the increase in RMS-EMG activity of the VL muscle. In support of this hypothesis, Kubo et al. [21] trained the knee extensors isometrically at either 50° or 100° of knee flexion. Based on their MVC and EMG recordings, they estimated that the internal force on the quadriceps muscles was 2.3 times greater at longer muscle lengths (i.e. 100°) than at shorter lengths. A further variable that must be considered is the influence of changing muscle lengths on the force-length relationship of muscle (for review see [23]). In short, when one alters the length of a muscle, the basic contractile units of individual muscle fibres, known as sarcomeres, also change length. The ability of sarcomeres (and thus muscle) to exert force is determined mainly by actin and myosin filaments interaction and cross-bridge formation. As sarcomere (or muscle) lengths increase, cross-bridges number and force is increased up to an optimal length. Beyond this length (i.e. with further lengthening), decreases cross-bridges formation and force are seen (NB. The caveat here is lies with contractile speed, and preceding type and

degree of muscle contraction [24]. If longer muscle lengths are less optimal for force production and cross-bridge formation than shorter muscle lengths, then greater motor unit recruitment will be necessary to overcome the external resistance. Therefore the two factors likely for greater activation in LL and LX compared to SL may be due to the greater internal mechanical stress on the muscle because of a shorter moment arm, and/or the length of the muscle reducing cross-bridge formation and force production per sarcomere, all other things (contraction type, speed and history) being equal.

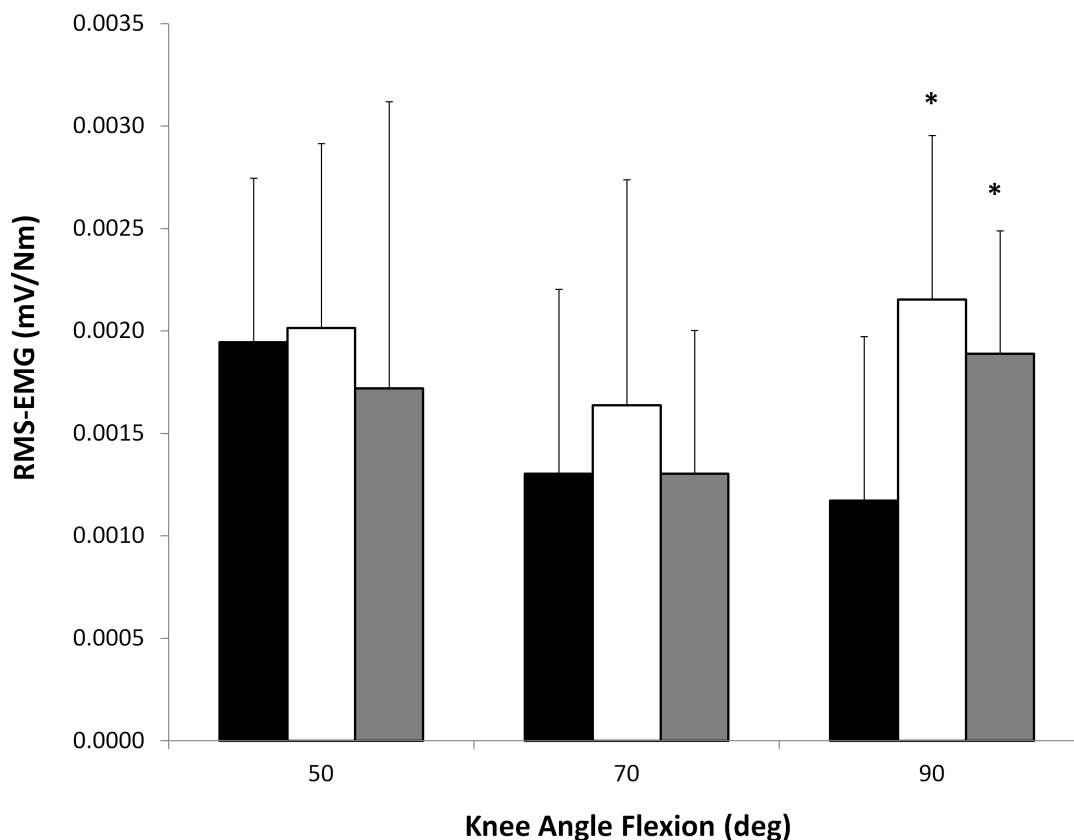


Figure 7. Vastus Lateralis muscle efficiency (i.e. activation per unit of torque) at week 8 at three joint-angles in SL (black bars), LL (white bars) and LX (grey bars). * Significantly different to SL ($P<0.05$). N.B. there were no between group differences at baseline.

In the current study, oxygen consumption (VO_2) was shown to be significantly greater at 80%1RM compared to 40% 1RM, and also significantly greater in both the LL and LX ROMs compared to SL ROM at 80% 1RM loading. VO_2 is used in exercise physiology to provide valuable information, such as an indicator of energy expenditure. Oxygen is 'consumed' by the working muscle during oxidative phosphorylation in order to produce, maintain and/ or replenish the energy used during the many different processes involved with muscular contraction. Therefore if a particular form of exercise requires the use of greater volumes of oxygen, this indicates that the system is working harder in order to meet the demands. It has been demonstrated previously in humans that oxygen consumption increases with work

intensity during constant isometric loading of the knee extensors [13, 14], and this is reflected by the increased VO_2 at 80% 1RM compared to 40% 1RM, where although performing the same ROMs, participants were exerting greater force, requiring more energy to supply muscular contraction. The relative VO_2 levels are much lower than normally encountered during aerobic exercise for example, due to the shorter duration of exercise bouts and greater contribution to energy supply from anaerobic sources such as ATP-PCr system and glycolysis. Of more interest in the present study was the fact that both LL and LX ROMs had significantly greater VO_2 compared to SL at 80% 1RM. Previous research using near-infrared spectroscopy has demonstrated that during isometric exercise of the knee extensors, VL muscle VO_2 is significantly increased at longer muscle lengths (60° and 90°) compared to shorter muscle lengths (30°). This was even despite the fact that MVC torque relative to the maximum torque capacity (MTC) tended to be greater (~85% of MTC) at 30° compared to both 60° and 90° (~75% MTC). A subsequent study by Kooistra et al. [14] demonstrated that knee extensor muscle activation and VO_2 were significantly less, and time to $\text{VO}_{2\text{max}}$ significantly longer at the same relative torque levels at 30° compared to 60° and 90°. An additional indication of the increased stress at longer muscle lengths was the observation that at 80% 1RM, although covering almost half the ROM of LX, LL group showed a trend (though not statistically significant) to consuming greater volumes of oxygen. This suggests that the energetic cost of constantly working at longer muscle lengths is at least just as, if not more demanding than, alternating between longer and shorter muscle lengths even when over a relatively large ROM. With significantly higher heart rates in both LL and LX groups (and also greater blood pressure in LX) compared to SL during exercise, the results also suggest that the cardiovascular system was also under greater stress at longer muscle lengths. Taken into consideration with both the aforementioned differences between the LL and LX groups compared to SL with regards muscle activation and oxygen consumption, it appears that performing exercise over predominantly longer muscle lengths (or incorporating longer muscle lengths into a full ROM) present a more potent stress to both neuromuscular and cardiovascular systems than performing exercise over mainly shorter muscle lengths. So what factors are present that would require greater oxygen consumption at longer muscle lengths? First of all, as mentioned previously, there are a number of processes that occur in order for a muscle to contract and produce force. One such process has been termed excitation-contraction coupling, where an action potential induces the release of calcium ions (Ca^{2+}) from the muscle membrane (sarcoplasmic reticulum) and these ions interact with the thin filaments of a sarcomere, allowing muscle contraction to occur. Ca^{2+} ions are then transported back into the sarcoplasmic reticulum for storage, allowing the muscle to relax. These processes are ATP-dependent (i.e. energy consuming) and as energy is consumed during activation, the amount of energy is measured as heat [25]. Therefore if greater activation of the muscle is occurring at longer muscle lengths, the possibility exists that the energy cost of this activation is also greater, and that this mechanism requires greater oxygen consumption to supply the energy. In addition, potentiation is force enhancement following muscle contraction, and is dependent on the contractile history. Place et al.[26] showed that following fatiguing contractions in the quadriceps muscles at either shorter (35°) or longer (75°) muscle lengths, peak twitch potentiation and doublet force were significantly greater at shorter muscle lengths, which may also allow for a reduction in energy cost as activation may be reduced.

Secondly, we have already discussed the likelihood that due to the internal architecture of muscles and tendons, that the length of the moment arm will dictate that greater muscle force will have to be produced at longer muscle lengths compared to shorter muscle lengths. Production of the additional force through recruitment of more motor units would mean that more of the contractile machinery would be used and be consuming energy, as muscular contraction from cross-bridge cycling also requires ATP [27, 28]. Therefore the additional oxygen consumption observed at longer muscle lengths may be the result of both the energetic requirements of muscle activation and the increased energetic requirements of force production. This hypothesis is consistent with the fact that endurance performance is significantly reduced with time to fatigue at longer muscle lengths compared to shorter muscle length, regardless of the intensities of loading and circulatory conditions [15, 26, 29]. Consistent with an increased oxygen demand, would be an increase in heart rate which was observed between the groups.

When exercise is performed on a regular basis, the above acute responses to a bout of exercise will eventually result in long-term adaptations (i.e. repeated bout effect), which will allow the body to complete the same exercise bout as before but with relatively less disturbance to homeostasis. During the resistance training program, the three groups performed exercise over the same range-of-motion as during the acute bouts (i.e. SL, LL and LX), with the only differences being the degree of loading. SL and LX exercised at 80% 1RM, whereas LL exercised at 55% 1RM, where this was to allow the length of muscle excursion (50°) and the internal muscle forces to be as similar as possible during resistance training between SL and LL. Following 8 weeks of resistance training, absolute changes in muscle activation did not increase significantly at any of the angles tested (50°; shorter lengths, 70° more optimal lengths, 90° longer lengths) during an isometric MVC. There have been conflicting reports throughout the literature concerning the possible increase in agonist activation following resistance training, as there have been studies published that have reported significant changes [3, 6-12], whereas some have not [30-33]. However, comparing longitudinal changes in agonist EMG both within and between studies can prove difficult due to methodological differences [34]. In one length-specific resistance training study, Thepaut-Mathieu et al. [19] reported an increase in iEMG-force relationships at the specific joint angles used during training. These findings were also supported by Kubo et al. [21] who found that iEMG of the quadriceps (rectus femoris, vastus lateralis and vastus medialis) increased significantly in groups that trained at either shorter or longer muscle lengths, with no differences between the groups at any of the joint-angles tested. In the current study there were also no significant differences in maximal activation levels between groups and muscle lengths. However, one of the main findings from the current study was the significant relative increases in activation at all muscle lengths in LX, at longer muscle lengths in LL, and significant decreases in activation at longer muscle lengths in SL. This is further evidence of the muscle length (or joint-angle) specificity phenomenon following resistance training. Whereas a previous study [21] found that relative quadriceps iEMG increased at all measured knee angles (40-110°) following 12 weeks of isometric resistance training at shorter muscle lengths, our results show a decrease in activation at longer muscle lengths occurred following training at shorter muscle lengths. Interestingly from the study of Kubo et al. [21] was the fact that although iEMG increased within the range of ~25-45% over

all testing angles (40-110°) following training at shorter muscle lengths, MVC only significantly increased between 40-80° in this group. Previous work from our laboratory has shown that MVC torque did not change significantly at longer muscle lengths following a period of resistance training at shorter muscle lengths [35], and results from the current investigation show that this could be in part be mediated by a reduction in maximal activation at these lengths. Further evidence of muscle-length specificity was the fact that only LX group, who covered an entire ROM, actually demonstrated a significant relative increase in activation at each angle tested, and also that LL only showed significant relative increases in activation at longer muscle lengths (lengths where the majority of training would have taken place). In order to allow us to describe the impact of changes in activation on strength changes, we have shown that there was significantly greater muscle efficiency (EMG per unit of torque) at longer muscle lengths (i.e. in LL and LX) compared to SL, following the 8-week training program. Changes in torque generating capacity are not accounted for solely, or at times at all by increased muscle activation. Changes in muscle architecture, morphology and/ or muscle specific tension are just a few of the many other factors that can impact a muscle's ability to produce force following resistance training as well as neural adaptations (for review see [34]). However in this case, there appears to be a relationship between the increased activation of the VL muscle and the changes in torque production following resistance training in LL and LX at longer muscle lengths.

As indicated above, one of the other factors influencing changes in torque or force production following resistance exercise is muscle morphology, such as size. There is a strong positive relationship between the size of a muscle and the force it is able to exert [1]. In the current study, all of the three training groups increased the size of the VL muscle at proximal (25%), central (50%) and distal (75% of femur length) measurement sites at week 8. However in the SL group, the muscle size increment was more significant centrally rather than at proximal and distal sites of the VL, whereas both LL and LX had fairly equal distribution of size increment along the length of the muscle. Firstly, this information suggests that the resistance training program was effective in increasing muscle size, which is a well established characteristic of resistance training. Secondly, the results also suggest that the ROM involved during resistance training (i.e. the muscle lengths used) may produce region specific variations in muscle growth. Our laboratory has provided more conclusive evidence that muscle size increments at distal regions are enhanced to a greater degree immediately following resistance training at longer muscle lengths [35], however in the current study this was only apparent following two weeks of detraining, although these were still present following a total of four weeks detraining. The region specific variation in muscle size has been previously documented throughout literature (e.g. [31]), and is probably due to the unique way in which forces are transmitted along the length of a muscle when exercised at different lengths. Forces in muscles are transmitted both serially and in parallel [36], and when training at longer muscle lengths, there may be a more pronounced parallel transmission of force at distal regions of the muscle, providing a stimulus for growth in this location. In terms of muscle growth, force production and muscle stretch are potent stimulators of muscle protein synthesis, with a combination of both having an additive effect [37]. In vitro experiments have shown that when muscle cells are stretched to longer lengths, there is a marked increase in protein synthesis and growth

factor mRNA [38]. The LL and LX groups when performing exercise at longer muscle lengths would have experienced a larger degree of muscle stretch compared to SL, and would have also been simultaneously producing force. In addition, because LX group worked at an intensity of 80% 1RM, peak force generation would also have been greater in this group. This is supported by the mean relative increase in VL muscle width being greatest in this group at all measurement sites, although due to the variation between subjects, this was not statistically significant. It is encouraging that despite the greater absolute force generations in LX compared to LL, the LL group (who remained at longer muscle lengths throughout each training session, and therefore muscle stretch would probably have persisted compared to LX group who worked between shorter and longer muscle lengths), these two groups exhibited similar muscle hypertrophy responses. What is more, yet another encouraging aspect of LL training was the fact that at week 10, VL muscle widths were significantly greater in LL and LX at all measurement sites compared to baseline, whereas the SL group had returned to baseline values. Following a further two weeks of detraining, LX group muscle widths only remained significantly greater than baseline values at 75% femur length, whereas LL group retained post-training increments in muscle width at all measurement sites for the entirety of the detraining period. Therefore not only does training at longer muscle lengths possibly confer more beneficial adaptations following training, but it also appears to allow retention of these adaptations for a longer period of time. This is a positive finding from the current study, in that following any periods on illness, injury or tapering that occur to the individual, longer-term retention of the benefits of the preceding resistance exercise will minimise the impact of such deleterious events.

5. Conclusion

Performing resistance training over predominantly longer muscle lengths compared to shorter muscle lengths produces stepwise degrees of acute muscular, energetic and cardiovascular responses, which then culminate to differential magnitudes of chronic training as well as detraining adaptations. As a progression to the earlier research evidence from isometric exercise in terms of both acute [13, 14] and chronic [21] muscle length-specific training, the current study is the first to systematically show that dynamic exercise at longer muscle lengths also results in greater activation and oxygen consumption. The nature of the acute responses suggests that the muscle is more physiologically stressed at longer muscle lengths. Following a prolonged period of resistance training (i.e. an accumulation of training bouts), we show that long-length trained muscle exhibits relatively greater muscle activation, neuromuscular efficiency and hypertrophy compared with its short-length trained counterpart. Similarly with detraining, long-length training was associated with a greater retention of improvements in muscle characteristics. It is likely that in this case also, the more beneficial size increments in particular, were the result of greater physiological stress, a result of the combined effects of smaller moment arm and enhanced muscle stretch. These findings have implications for athletic, elderly, or post-operative populations to name but a few end users.

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